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Impact of warming and deoxygenation on the habitat distribution of Pacific halibut in the Northeast Pacific

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Ocean warming and deoxygenation are already modifying the habitats of many aerobic organisms. Benthic habitat in the Northeast Pacific is sensitive to deoxygenation, as low oxygen concentrations occur naturally in continental shelf bottom waters. Here we examine the potential impacts of deoxygenation and ocean warming on the habitat distribution of Pacific halibut (*Hippoglossus stenolepis*), one of the most commercially-important groundfish in North America. We combine fisheries-independent Pacific halibut survey data (1998 – 2020) with oceanographic measurements and a regional ocean circulation model to investigate current and future (end of 21^{st} century) influences of deoxygenation and warming on optimal Pacific halibut habitat. We use the observations and model output to derive a metabolic index of Pacific halibut-specific suitable habitat. Our results show high Pacific halibut counts in regions where the metabolic index is greatest, and demonstrate that interannual variability in Pacific halibut abundance is coherent with the Pacific Decadal Oscillation. Working with model projections, we examine potential future changes in suitable Pacific halibut habitat by the end of the century under a

high carbon dioxide emissions scenario. These projections indicate that suitable Pacific halibut habitat may largely disappear off the coast of Washington state, retreating approximately five degrees latitude northward. In bottom waters along coastal British Columbia and Alaska continental shelf, Pacific halibut habitat is projected to decrease by about 50%. Such habitat changes may potentially drive a northward shift in Pacific halibut, with significant implications for commercial fisheries.

KEYWORDS
Pacific halibut, Metabolic index, oxygen demand, ocean warming, ROMS, Subarctic Pacific

1 | INTRODUCTION

Ocean warming and deoxygenation are already modifying habitat availability for many aerobic organisms, with significant impacts on their distribution over space and time (Cheung et al., 2009; Keeling et al., 2010; Seibel, 2011). A number of studies have analyzed the response of marine species distributions and ecosystem structure to increasing temperature (Campana et al., 2020; Christian and Holmes, 2016; McLean et al., 2018; Perry et al., 2005; Sunday et al., 2015), but less work has considered the impact of concurrent warming and deoxygenation in driving habitat reduction (Bianucci et al., 2015; Deutsch et al., 2015, 2020; Howard et al., 2020b; Thompson et al., 2022).

From both a physiological and oceanographic perspective, oxygen availability and temperature are closely linked. Physiologically, the metabolic oxygen demand of aerobic organisms rises with increasing temperature (Pörtner and Knust, 2007), such that deoxygenation has greater impacts on organismal growth and survival under high temperature conditions (Deutsch et al., 2015, 2020). At the same time, higher temperature favors oxygen loss by decreasing seawater oxygen solubility and increasing stratification, which limits the ventilation rate of thermocline water masses (Franco et al., 2021; Kwon et al., 2016; Ono et al., 2001; Sasano et al., 2018). Among all oceanic regions, the Northeast Pacific exhibits one of the most rapid apparent rates of deoxygenation (Keeling et al., 2010; Schmidtko et al., 2017), with large oxygen decreases projected for intermediate depths over the coming decades (Long et al., 2016). This ocean region has already lost approximately 15% of its oxygen inventory over the past 60 years (Ross et al., 2020), but it is presently unclear how ecosystem structure and species distributions have been impacted.

The habitat of benthic organisms is particularly sensitive to deoxygenation (Levin et al., 2009; Ross et al., 2020; Yati et al., 2020) since low oxygen concentrations occur naturally in the subsurface waters due to respiration of organic matter. Near the coast, increased nutrient input and subsequent eutrophication, exacerbate coastal deoxygenation and modify nutrient and microbial cycles (Breitburg et al., 2018; Gilly et al., 2013; Howarth et al., 2011). Among fish species, groundfish, which spend the majority of their adult life near the ocean floor, are thus most susceptible to oxygen depletion. For example, a recent study using numerical biogeochemical ocean models and fisheries observations showed that future anthropogenic deoxygenation and warming may drive biodiversity changes on groundfish species in the North Pacific (Thompson et al., 2022). Similarly, Bianucci et al. (2015) demonstrated that decreasing oxygen concentration in the Gulf of St. Lawrence led to a reduction in the optimal habitat of the groundfish Atlantic wolffish

and associated changes in its distribution. Using similar numerical and observational tools and accounting for future projected changes in temperature and oxygen, Clarke et al. (2021) showed that commercially-important fisheries in the Eastern tropical Pacific will also be affected by habitat contraction. Howard et al. (2020b) estimated that ocean warming and deoxygenation can potentially drive widespread extirpation of northern anchovy, a key forage species in the California Current System.

Commercial groundfish fisheries account for approximately 50% of the total fish landings in the US (Lehodey et al., 2006). The Pacific halibut (*Hippoglossus stenolepis*) fishery is one of the most important commercial groundfish fisheries along the Northwest coast of the United States and Canada (Haigh et al. (2015), their Figure 4). This species is distributed over the majority of the North American Pacific coast, from central California to the Bering Sea (Sadorus et al., 2021), and is regulated and surveyed by the International Pacific Halibut Commission (IPHC). Since 1997, the number of Pacific halibut counted in fisheries-independent surveys has declined persistently along the entire IPHC regulatory areas, from Alaska to California (Stewart and Wilson, 2020). Regionally, however, Pacific halibut catch per unit effort (CPUE) in the coastal waters of California, British Columbia, and Southeast Alaska, has varied significantly across years, with no apparent trend between 1992 to 2019 (Stewart and Wilson, 2020).

A number of oceanographic variables, including bottom depth, temperature and dissolved oxygen are all likely important factors influencing Pacific halibut distribution and abundance (Sadorus et al., 2014). To date, however, there have been few studies explicitly examining regional-scale links between oceanographic conditions and Pacific halibut abundance. Earlier work demonstrated that interannual variability in Pacific halibut recruitment, growth and distribution may be linked to the Pacific Decadal Oscillation (PDO) (Mantua et al., 1997; Francis and Hare, 1994), an index describing a pattern of ocean-atmosphere variability. In the Northeast Pacific, a positive PDO phase translates into warmer surface temperatures and higher stratification, while the opposite occurs during a negative (i.e., cold) phase (Chhak and Di Lorenzo, 2007). Using one of the longest Pacific halibut time series available (1935 to 1994), Clark and Hare (2002) showed that the abundance of the six-year age class Pacific halibut increased when the fish were spawned during positive regimes of the PDO, while the opposite occurred during negative phases of the PDO. This result suggests that processes driven by the PDO may influence the synchrony between groundfish spawning, recruitment and climatic indices (Lehodey et al., 2006). However, the underlying factors driving this empirical relationship remain unknown.

Here we build on previous work, combining fisheries-independent survey data with oceanographic observations and a regional ocean model to examine the relationship between environmental factors and Pacific halibut CPUE. We focus particular attention on the relationship between Pacific halibut distribution and the oxygen and temperature properties in coastal ocean bottom waters off California to Southeast Alaska. By examining the historical trends, present-day spatial distributions, and potential future trajectories, our goal is to explore potential climate change impacts on the future distribution of Pacific halibut habitat and habitat suitability in an ecological and economically important ocean region.

2 | DATA AND METHODS

2.1 | Pacific halibut data

Observations of Pacific halibut CPUE were obtained from the IPHC Fishery-Independent Setline Surveys (FISS) (https://www.iphc.int/data/fiss-data-query), for the subareas 2A (off California, Oregon and Washington, USA), 2B (off British Columbia, Canada) and 2C (off Prince of Wales Island, Alaska, USA). These subareas (shown in Figure 1) were operationally established by the IPHC in 1990 for the management of the fishery. Each subarea extends 200

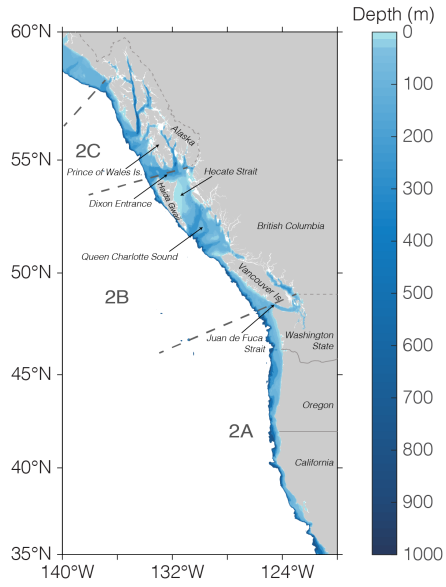

FIGURE 1 Reference map showing the IPHC Regulatory subareas 2A, 2B, and 2C and other relevant geographical features. The color scale represents the ocean bathymetry in the Pacific halibut sampling region up to 1000 m depth. Dashed lines on land indicate the Canada - USA borders, while dashed lines in the ocean indicate IPHC subarea boundaries. The southern boundary of subarea 2A extends to the international border between US and Mexico, however, the FISS stations are limited to north of 37°N.

nautical miles offshore, but the majority of the sampling stations are located over the continental slope within 150 km (approximately 80 nautical miles) from the coast.

Most sampling stations were visited each summer (June – August), when Pacific halibut approach the coast to feed (Skud, 1977). The majority of the stations were sampled at least 20 times over the 23-year period of the time series, and only stations sampled more than five times over the sampling period (1998-2020) were used to derive long-term CPUE summer means. The number of times each station was visited over the sampling period is shown in Figure S1. With this criterion, we included 106 stations sampled in subarea 2A, 170 stations in subarea 2B and 123 stations in subarea 2C. The model grid used to assess the temperature and oxygen characteristics of each region (see Section 2.3) does not resolve the inshore waters of the coastal fjords (Figure S2). For this reason, we excluded the innermost FISS stations when co-locating fisheries data with model-based environment data (Section 3.1.3). Most of these inner stations correspond to stations with the lowest Pacific halibut counts.

The Pacific halibut survey data are normalized by the Catch Per Unit Effort (CPUE), which is based on the number of effective skates hauled, and where 1 skate is approximately 100 hooks. We report the data as individuals per skate (ind./skate), i.e., the CPUE, which may be used as an index of relative abundance, rather than absolute abundance (Maunder et al., 2006; Thompson et al., 1998). Sampling details are indicated in the IPHC Fishery-Independent Setline Survey Sampling Manual (IPHC, 2021). Pacific halibut CPUE is reported for two size classes; fork lengths greater or less than the minimum legal-size limit of 32 inches (81.3 cm). In the following, we consider each size class independently and refer to each as over 32 inches (O32) or under 32 inches (U32).

2.2 | Hydrographic data from IPHC

Starting in 2009, hydrographic data (temperature, salinity and dissolved oxygen) have been recorded alongside the Pacific halibut longline surveys described above. These environmental data were collected at most of the FISS stations with calibrated SBE19plusV2 water column profilers (Sadorus et al., 2016). We used the deepest readings from each profile (estimated to be 5-15 m from the sea bottom) as provided from the IPHC data request portal (https://www.iphc.int/data/fiss-data-query). The environmental data reflect the environmental conditions of Pacific halibut habitat at the time of sampling, and were used to estimate critical statistical parameters describing the suitable aerobic habitat of Pacific halibut (see Section 2.4).

2.3 | Model description and simulations

To assess the impact of present-day variability and potential future changes in the habitat distribution of Pacific halibut, we used monthly output from two regional ocean model simulations: 1) a hindcast simulation representing the period 1994 – 2007, with spatial resolution of 12 km over the whole domain of the IPHC subareas 2A, 2B and 2C; and 2) a 12 km resolution future simulation for the same domain, representing late 21^{st} century conditions under the Representative Concentration Pathway (RCP) 8.5 (high CO_2 emissions scenario). Currently, the historical total cumulative CO_2 emissions are consistent with the CO_2 emissions considered in the RCP8.5 (Schwalm et al., 2020). It is expected that continuing on the RCP8.5 path will lead to a global mean surface air temperature increase of approximately 4°C (relative to 1986-2005) by the end of the century (Collins et al., 2013), resulting in a large decrease in seawater oxygen solubility and concentration (Oschlies, 2021). Each Pacific halibut sample was co-located with simulated temperature, O_2, and Φ in space and time over the period of overlap between the fisheries surveys (1998-2020) and the hindcast model simulation (1994-2007).

The model simulations are based on the Regional Ocean Modeling System (ROMS) (Shchepetkin and McWilliams, 2005), coupled to the Biogeochemical Elemental Cycling (BEC) (Moore et al., 2001, 2004). The model is configured for the California Current System (CCS), and uses a spherical grid with horizontal resolution of 12 km, and a vertical resolution of 42 terrain-following layers covering the region from 20°N to southeast Alaska (60°N), and from the coast to 3000 km offshore (Figure S2). The physical and biogeochemical parameters are those described in Renault et al. (2021) and Deutsch et al. (2021), respectively. A complete description of the forcing and boundary conditions for the hindcast and future simulation is provided in Howard et al. (2020a) (see their Table 1).

2.3.1 | Model evaluation

Previous work with the 12 km model simulations described above, and comparison with a set of closely related higher resolution (4 km) simulations, has shown that the 12 km simulation successfully captures key climate responses (Howard et al., 2020b). The model also accurately reproduces the annual mean World Ocean Atlas 2018 (WOA18) temperature and oxygen distributions (Garcia et al., 2018; Locarnini et al., 2018) in the region of the California Current System (Deutsch et al., 2021; Howard et al., 2020b; Renault et al., 2021). Since the Pacific halibut surveys used in this study were conducted in summer (typically, June, July and August), we extended the previous evaluation to specifically assess model skill in resolving the summer climatology of oxygen and temperature distributions (Figures 2 and S3). We also extended our quantitative evaluation of the model performance to include the region off southeast Alaska. To evaluate the model, we used climatological summer oxygen and temperature fields from the WOA18, as well as oxygen and temperature profile data from the World Ocean Database 2018 (Boyer, 2018) to evaluate the

simulated vertical structure (Figure S4).

In general, we found that the model effectively captures the observed large-scale summer features of temperature and oxygen across our study domain (Figure 2). At 100 m, the model agrees well with the observed large-scale North-South temperature gradient over the fisheries subareas 2A, 2B and 2C (Figure 2a-c). In the nearshore region (within 100 km from the coast), the simulated temperature in our region of interest between 35 and 58°N agrees exceptionally well with the observations, with a mean temperature difference for the summer climatology of only 0.02°C. At 200 and 300 m, the model produces slightly colder waters than observed in the nearshore, but this difference is less than 0.4°C across all three subareas (Figure S3), and only 0.2°C for subarea 2C (between ~ 54 and 58°N).

The overall simulated oxygen and temperature vertical structure is consistent with the observations (Figure S4). However, the model tends to underestimate the observed oxygen concentration on average (Figure S3b), with the largest discrepancies (up to 35 µmol L^{-1}) at 100 m within 100 km from the coast. At 200 and 300 m, the bias between the model and the observations is smaller (28 and 19 µmol L^{-1}, respectively), and the simulated spatial pattern is consistent with the observations. Some of these discrepancies might stem from the scarcity of summer observations used to generate the World Ocean Atlas climatology, particularly in the region off Haida Gwaii and Prince of Wales Island (See inset in Figure S4a). Additionally, this negative bias may be the result of previously identified mismatches between modeled and observed density fields stemming from the boundary conditions (Deutsch et al., 2021; Howard et al., 2020b; Renault et al., 2021).

2.4 | Definition of suitable aerobic habitat

As an indicator of Pacific halibut-specific suitable aerobic habitat, we used a recently revised Metabolic Index (Φ; (Deutsch et al., 2015, 2020), which estimates the ratio of ambient oxygen supply ($O_{2,supply}$) to Pacific halibut O_2 demand ($O_{2,demand}$) at a resting metabolic rate:

$$\Phi = \frac{O_{2,supply}}{O_{2,demand}} = A_0 \frac{pO_2}{exp(-E_0/k_B(\frac{1}{T} - \frac{1}{T_{ref}}))} \quad (1)$$

This index is calculated based on ambient temperature (T, °K) and oxygen partial pressure (pO_2, atm^{-1}), the Boltzmann constant (k_B, eV), as well as ecophysiological parameters: the hypoxia tolerance (A_0, atm^{-1}) that applies at a reference temperature (T_{ref} = 15°C), and the temperature sensitivity to hypoxia tolerance (E_0, eV). For the habitat to be aerobically viable, the $O_{2,supply}$ must at least meet the $O_{2,demand}$ of a species. This condition restricts organisms to waters with a pO_2 above a minimum critical value. For resting metabolism, this threshold is typically measured via laboratory respirometry (an extensive summary of respirometry studies is provided in Deutsch et al. (2020)). For active metabolism required to sustain a population, the temperature-dependent minimum pO_2 can be estimated as that which bounds the geographic range of a species (Howard et al., 2020b). The resulting parameters yield a Φ scale that is normalized to an active ecological threshold (often denoted Φ_{crit}; (Deutsch et al., 2015, 2020; Howard et al., 2020b) rather than the physiological threshold of laboratory conditions.

To estimate the active and temperature-dependent hypoxia tolerance of Pacific halibut, we considered the observed T and O_2 conditions in those locations with occurrences of Pacific halibut (sampled concurrently, see Section 2.2) over the full IPHC monitoring region (Figure 3a). Projecting species occurrences across the range of joint temperature and pO_2 conditions reveals that the lowest pO_2 inhabited by Pacific halibut is dependent on temperature, an observation common to most species (Deutsch et al., 2020). The parameters of Φ (i.e., A_0 and E_0 from Eqn. 1) are

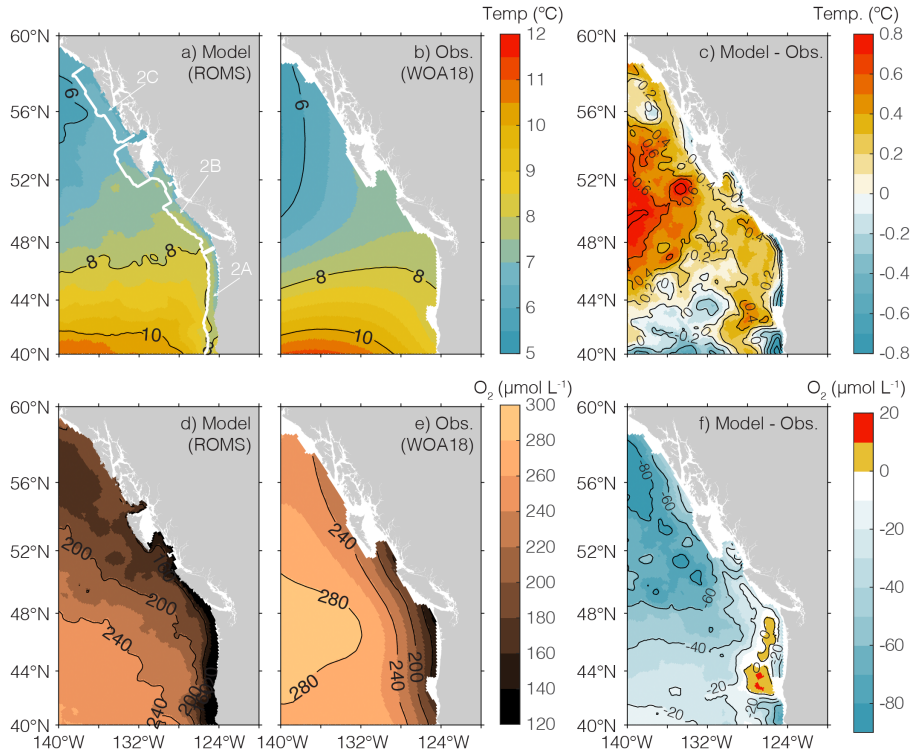

FIGURE 2 Climatological summer (June-July-August) temperature (a-c) and oxygen (d-f) at 100 m depth, where Pacific halibut is abundant. The left panels show the model derived summer climatology (1994-2007). The middle panels show the summer climatology from the World Ocean Atlas (WOA18) re-gridded to the 12 km ROMS resolution. The difference (model minus observations) is shown in the right column. The white line on panel a) is the 100 km nearshore region for each IPHC subarea (2A, 2B, and 2C) used in the statistical analyses of Figure S3.

those which optimally delineate the inhabited and uninhabited regions in the state-space of temperature and pO_2 (dashed line in Figure 3b), such that the realized niche has $\Phi > 1$ while conditions with no species occurrences have $\Phi < 1$. When fitting the model, the optimal parameters are chosen to maximize the F-score of the habitat categorization (Deutsch et al., 2020; Shawe-Taylor and Cristianini, 2004).

Once all the ecophysiological parameters were derived, Φ was estimated based on the summer mean temperature and oxygen from the present and future simulations described in Section 2.3. The distribution of the estimated values is similar between the ROMS-derived Φ (calculated for the period 1998 - 2007) and observation-derived Φ (calculated for the period 2009-2020) (Figure S5). This agreement provides further reassurance that, despite the moderate simulated underestimation of oxygen concentration in the water column (e.g., Figure 2f), the model performs well when translating the temperature and oxygen concentrations from the benthic habitat to the ecologically-relevant metabolic index.

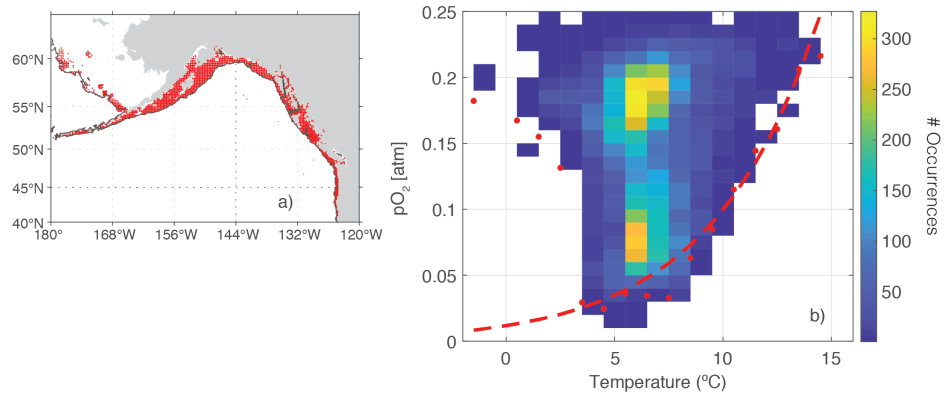

FIGURE 3 a) Full geographical range of the IPHC Fishery Independent Setline Survey stations with near ocean floor temperature and oxygen measurements. b) temperature and oxygen partial pressure state-space at the locations shown in a) where Pacific halibut was present. The lowest pO_2 associated to a given temperature class is indicated in red dots. The fitted model used to derive the Φ ecophysiological parameters (A_0 = 3.65 atm^{-1} and E_0 = 1.42 eV) is shown in dashed-red.

3 | RESULTS

3.1 | Regional oceanography and spatial Pacific halibut distribution

3.1.1 | Summer oxygen, temperature and Φ

To a large extent, coastal upwelling and downwelling define the oxygen and temperature features of the west coast of the United States and Canada (Ware and McFarlane, 1989). In the southern subareas (2A and 2B, Figure 1), off California, Oregon, Washington, and southern British Columbia, summer upwelling brings cold, low oxygen subsurface water with subtropical influence to shallower depths (Adams et al., 2013; Ianson et al., 2003). Further north off southeast Alaska (subarea 2C), coastal downwelling of subarctic water is persistent throughout the year, although weaker in the summer months (Ware and McFarlane, 1989). The spatial pattern of northern downwelling and southern upwelling in our study region partially contributes to latitudinal gradients in oxygen and temperature. In summer, temperature at 100 m generally decreases northward from 8.2 °C in subarea 2A to 6.5 °C in subarea 2C (spatial mean of the 100 km nearest to the coast for each subarea), while oxygen increases from 140 µmol L^{-1} to 245 µmol L^{-1} (Figure 2b,e). This latitudinal gradient is also apparent (although weaker) at 200 m and 300 m (not shown), and is reflected in an overall northward increase in Φ (Figure S6a,d,g), which is mainly driven by the spatial distribution of oxygen. At 100 m, the difference between subarea 2A and 2C is notable, with a mean Φ of 1.4 and 2.9 in the nearshore waters of subareas 2A and 2C, respectively. As with oxygen, the latitudinal Φ gradient becomes weaker with depth; at 300 m, in the northern subarea (2C) Φ is only 0.4 units higher than the value in the southern subarea 2A.

Water properties at the deepest layer of the water column (i.e., benthic habitat), where Pacific halibut tend to be found, are shown in Figure 4. Temperatures above the 5th percentile (p5) of the Pacific halibut distribution (3.7 °C) occur over most of the domain, from California to southeast Alaska. Oxygen above the p5 (a concentration of 63 µmol L^{-1} or O_2 partial pressure of 0.04 atm) is more prevalent across the northern region of the domain (Figure 4b). South of 45 °N, ocean bottom oxygen concentrations in summer are lower. As in the water column (Figure 2), ocean bottom temperature decreases and oxygen increases northwards, with the exception of shallow (< 100 m),

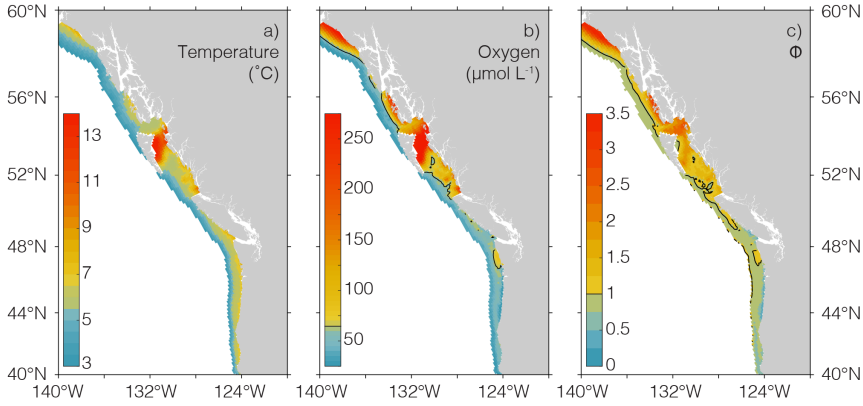

FIGURE 4 ROMS-based mean (1994-2007) summer (June-August) ocean bottom temperature (a), Oxygen (b) and Metabolic index, Φ (c). The contours in b) and c) indicate the value above which 95% of the Pacific halibut sampled at the FISS was found. i.e., the 5^{th} percentile (p5). The p5 is 63 µmol L^{-1} (pO_2 of 0.04 atm at the p5 temperature and salinity) for dissolved oxygen, and 1.05 for Φ. Properties are shown for bathymetry shallower than 1000 m.

semi-enclosed Hecate Strait (Figure 1), where temperature is approximately 10 °C higher than the surrounding ocean bottom waters. In this shallow water column, strong tidal mixing (Perry et al., 1983) allows oxygenation so that oxygen values are similar to those near the surface (> 200 µmol L^{-1}; Figure 4b). In the coastal region north of 45 °N, lower temperatures and higher oxygen results in viable habitat for Pacific halibut, as demonstrated by the ocean bottom Φ values higher than the Φ_{crit} value of 1 (Figure 4c).

3.1.2 | Pacific halibut distribution

Pacific halibut in the O32 size class (i.e., individuals with fork length equal to or greater than 32 inches) concentrate in the depth range of 100 – 300 m (Figure S7a) along the west coast of Oregon, Washington, British Columbia, and southeast Alaska (Figure 5a). Within this depth range, the overall mean Pacific halibut CPUE (for subareas 2A, 2B and 2C) is 4.7 ind./skate. By comparison, the mean CPUE of O32 Pacific halibut at depths shallower than 100 m or deeper than 300 m is 2.9 ind./skate and 2.7 ind./skate, respectively. Smaller (U32) Pacific halibut (likely representing younger fish) were found in shallower waters concentrated in the range from 0 to 200 m depth (Figure 5b and S6b), with a mean of 3.2 ind./skate. The mean U32 CPUE below 200 m was lower, 1.5 ind./skate.

Regionally, the CPUE for both size classes of Pacific halibut are highest in the IPHC subarea 2C, with an overall mean of 6.7 ind./skate (O32) across all depths. Within this subarea, there is an apparent region of higher Pacific halibut density in the oceanic region off Prince of Wales Island and extending to Dixon Entrance (Figure 5a, see Figure 1 for annotations). Intermediate CPUE values were found in subarea 2B off British Columbia, with an overall mean O32 of 3.7 ind./skate. In this region, O32 and U32 Pacific halibut appear to concentrate in Queen Charlotte Sound and Hecate Strait (the region between Haida Gwaii and the northern tip of Vancouver Island, Figure 1). The lowest Pacific halibut CPUE were found off Oregon and Washington in subarea 2A (overall O32 mean of 1.5 ind./skate).

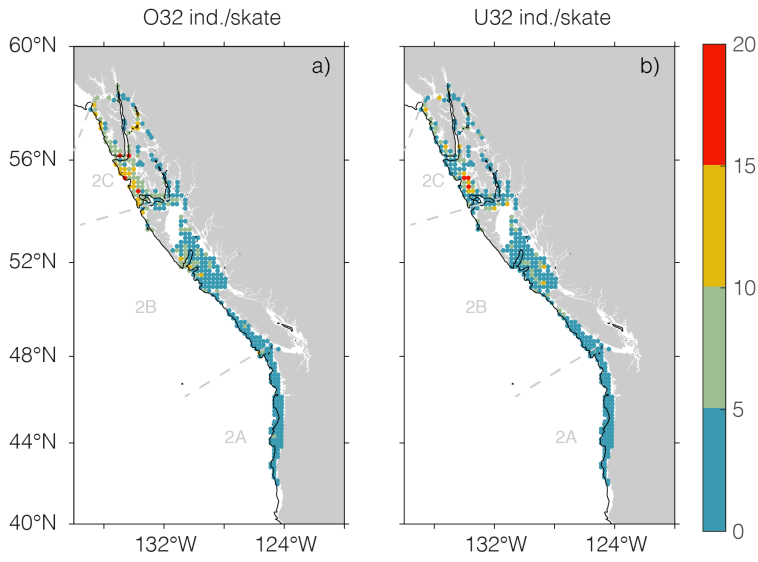

FIGURE 5 Summer average (1998 – 2020) distribution of a) O32 and b) U32 Pacific halibut across the IPHC survey stations. Each data point represents a time series station. The black contour denotes 300 m bathymetry. IPHC subareas are indicated.

3.1.3 | Pacific halibut distribution and Φ

We used fisheries data and space and time co-located model output to examine the relationship between Pacific halibut CPUE, temperature, O_2 concentrations, and Φ. We segregated the Pacific halibut CPUE into model-based Φ bins of 0.5, and calculated the mean CPUE for each group (Figure 6a,b). From this analysis, we found that the U32 and O32 size classes are related with oxygen, temperature, and Φ to varying degrees. The maximum O32 CPUE was found in waters with Φ values higher than 1.5, where the mean CPUE at the 1.5-2 Φ class was 7.1 ± 6.6 ind./skate. For U32, the maximum values were found in water with higher Φ (2.5 – 4), with a mean CPUE of 8.9 ± 6.4 ind./skate. The higher Φ associated with maximum U32 values partially reflect the shallower depth preferences of these smaller fish (Sadorus et al., 2014) (Figure S7b).

Results similar to those presented above were obtained from an analysis with observed environmental data sampled concurrently with the Pacific halibut but conducted over a different period (2009-2020; see Section 2.2 and Figure S5). As expected, the comparison of fisheries data with both model output and oceanographic observations indicates a strong relationship between Pacific halibut and Φ over the period between 1998 – 2020.

3.2 | Temporal variability in habitat distribution and CPUE of Pacific halibut

We did not identify any significant long-term regional trend in mean Pacific halibut CPUE over the period 1998-2020 (not shown). However, interannual variability in O32 was observed in subarea 2C (Figure 7a), with two periods of time with elevated O32 CPUE (1.5-2 ind./skate above the long-term mean) over the years 2000-2005 and 2012-2019. This interannual variability in O32 Pacific halibut was correlated with the Pacific Decadal Oscillation (PDO; $r = 0.46$, $p < 0.1$).

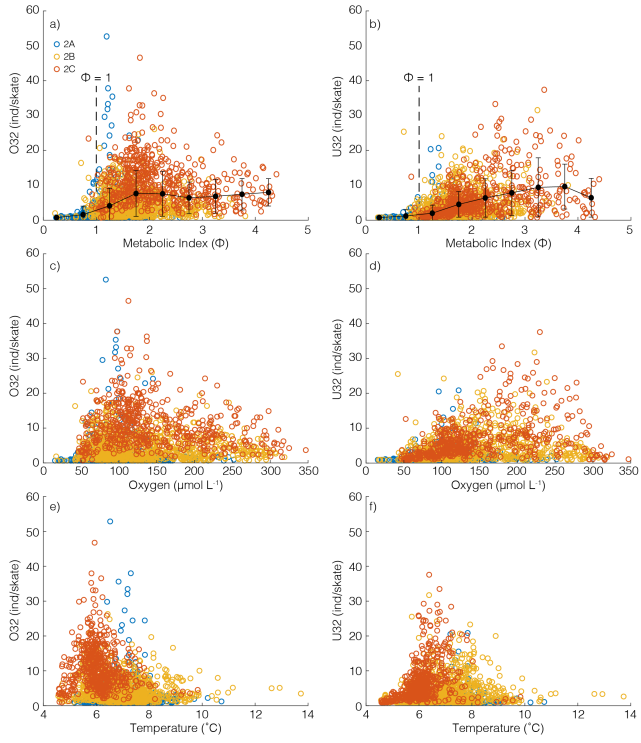

FIGURE 6 Relationship between model-derived Φ (top row), oxygen (middle row), and temperature (bottom row), and Pacific halibut over 32 inches (O32; left column) and under 32 inches (U32; right column). Oxygen, temperature, and Φ were extracted based on the date (month and year), depth, and geographic location of the Pacific halibut survey samples over the period 1998-2007. The black points and trend line in a) and b) indicate the mean and standard deviation in Pacific halibut CPUE for each 0.5 Φ class. The vertical dashed lines indicate the Φ_{crit} = 1, which represents the minimum value necessary for active metabolism (see section 2.4).

During the Pacific halibut survey (1998-2020), the PDO was predominantly negative (Figure 7), with the exception of two positive episodes: around year 2004 and more recently between 2014 and 2017. These two instances of positive PDO roughly correspond to the period of higher O32 Pacific halibut CPUE observed in 2C. In contrast, no statistically-significant relationship between Pacific halibut CPUE and PDO was apparent in more southern subareas 2A or 2B, where Pacific halibut CPUE was overall lower. Similarly, there was no significant relationship between PDO and U32 CPUE in any subarea analysed (Figure S8).

The model simulation was able to accurately reproduce interannual shifts in surface oceanographic variables related to the PDO (Figure S8). In subareas 2C and 2B, sea surface temperature tends to increase during the positive PDO phase (Figure S8a), while surface water oxygen and Φ tend to show negative anomalies (relative to the 1994-2007 simulated climatology). The opposite is true over periods when the PDO was mainly negative (e.g., between 1997 to 2003). The correlation of environmental variables with the PDO index is restricted to the surface layer (approximately top 50 m). In contrast, temperature, oxygen, and Φ in the Pacific halibut habitat (near ocean bottom waters) do not appear related to variations in the PDO (r = 0.04; Figure 8).

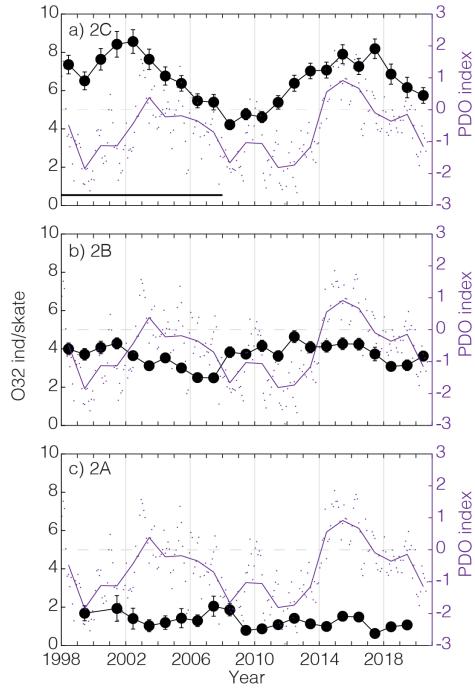

FIGURE 7 Annual time series of mean O32 Pacific halibut in subareas a) 2C, b) 2B, and c) 2A. The error bars denote the standard error of the spatial mean. The annual mean PDO (solid line) and the monthly values (individual markers) are also shown (right hand axis). The horizontal black line in panel a) indicates the overlapping period between the fisheries observations (1998-2020) and the model simulation (1994-2007). The dashed horizontal grid line indicates a value of the PDO index of zero.

3.3 | Future projections

Model simulations provide the opportunity to explore future environmental scenarios and their potential impact on Pacific halibut distributions. In RCP8.5 (high CO_2 emissions) simulations representing the end of the 21^{st} century, ocean bottom temperature increases by more than 1.5 °C along the coast and up to 3 °C in shallow regions such as Hecate Strait (Figure 9c). This warming leads to a projected displacement of waters with Pacific halibut-favored temperature (p50, 5.9 °C) further offshore to deeper depths (Figure 9b). Simulated oxygen concentration is projected to decrease everywhere, and the area with ocean bottom O_2 concentrations above the O_2,p5 (63 µmol L^{-1}) will be reduced to a narrow coastal band in Queen Charlotte Sound, off Prince of Wales Island and in Hecate Strait (Figure 9e). This reduction in O_2 is the main driver of the overall decrease in ocean bottom Φ projected for the end of the 21^{st} century, as can be seen in the similarity of the O_2,p5 and the Φ = 1 contours (Figure 9e,h). The area with suitable habitat to sustain active metabolism of Pacific halibut (Φ > 1) is projected to disappear everywhere south of Vancouver Island. This change translates into approximately a five degrees latitude northward retreat of the southernmost boundary of Pacific halibut suitable habitat. Further north, suitable habitat will be restricted to the coastal region off Hecate Strait and Prince of Wales Island.

To determine future changes in the extent of Pacific halibut habitat, we analyzed the change in the volume of

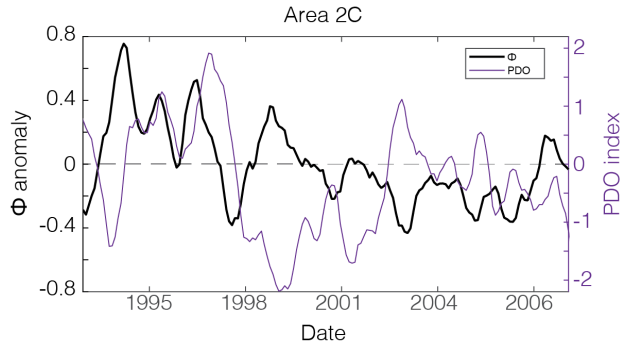

FIGURE 8 Time series of model-based bottom water Φ anomalies for the subarea 2C for the period of the model simulation (indicated in Figure 7a). The PDO index is shown in the right axis, with the horizontal dashed line indicating a PDO index of zero. The time series were averaged spatially over a region delineated by the 300 m isobath. Both time series were smoothed using a 6-months moving average.

bottom waters with different Φ values. For this analysis, we focused on the bottom layer of the model above the ocean floor, in a region delimited by the 300 m isobath for each IPHC subarea considered (Figure 10). We found that the volume of water below the Φ_{crit} (Φ = 1) in summer will at least double by year 2100, considerably limiting the potential habitat for Pacific halibut in the future in subareas 2B and 2C. In subarea 2B off British Columbia, unsuitable habitat will occupy approximately 90% of the layer above the sediments around the year 2100, as compared to 40% in the present day. Further north (subarea 2C) projected impacts are similar, with 80% of the benthic habitat below the Φ_{crit} by year 2100, as compared to only 20% at present. These results strongly suggest a potential future shift in Pacific halibut distribution to the northern range of our study region.

4 | DISCUSSION

Given the commercial importance of the Pacific halibut fishery, changes in the abundance and distribution of this benthic species will have significant economic consequences. By combining fisheries surveys of Pacific halibut with oceanographic data and output from an ocean biogeochemical model, we examined the potential impacts of deoxygenation and ocean warming on habitat availability for Pacific halibut. Our results show a clear spatial coherence between Pacific halibut and present-day oxygen, temperature and Φ at the southernmost boundary of their distribution range. Using model-based projections, we examined future potential contraction of preferred habitat, and assessed how the spatial distribution of Pacific halibut would change.

4.1 | Spatial and temporal variability

The time series of spatially-resolved and fisheries-independent IPHC Pacific halibut CPUE allow us to examine temporal and spatial relationships between the distribution of Pacific halibut and ocean bottom oxygen and temperature. Based on an analysis of more than two decades of observations, our results demonstrate a strong spatial relationship between Pacific halibut CPUE, O_2, and derived Φ values (Figure 6). These results agree with the previous work of Sadorus et al. (2014), who examined a shorter time series (2006 – 2009), and found that dissolved oxygen, and to a

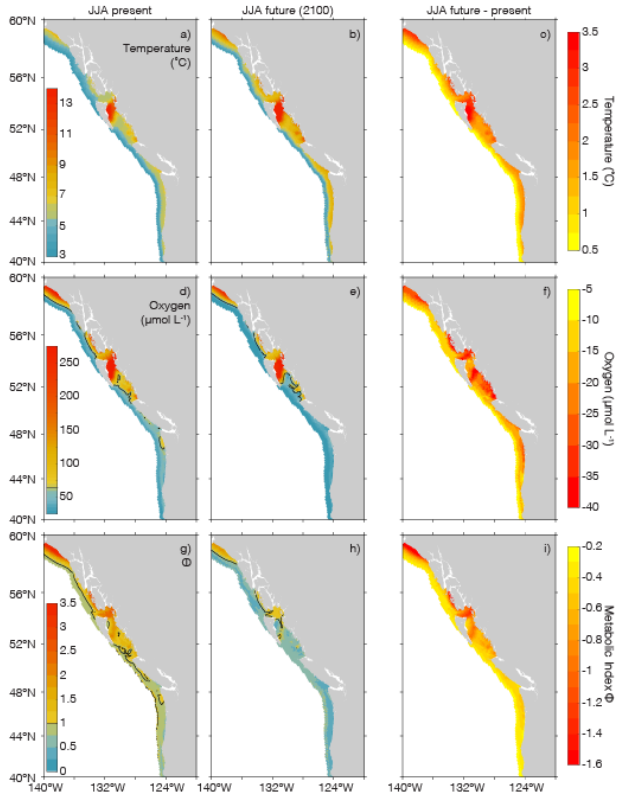

FIGURE 9 Ocean bottom temperature (top row), oxygen (middle row) and Φ (bottom row) for the summer mean over 1994-2007 (left column), future projection centered around year 2100 (middle column), and future change (future - present). The contours indicate the p5 for oxygen (63 µmol L^{-1} or a pO_2 of 0.04 atm at the p5 conditions of temperature and salinity) and Φ (1.05). The figures in the left column are the same as those in Figure 4.

lesser extent temperature, are key variables explaining Pacific halibut distribution off the US west coast and Southern British Columbia.

Our analysis of individual sampling stations and aggregated IPHC subareas indicate that there has been no significant trend in Pacific halibut CPUE in our study zone over the period 1998-2020. However, there is apparent co-variability between the PDO and mean regional summer O32 abundance in subarea 2C (Figure 7a). This relationship is sustained, although weaker (Pearson = 0.33) when O32 biomass (lbs/skate; not shown), rather than O32 abundance (ind./skate), is considered. Relationships between Pacific halibut growth and recruitment and North Pacific climatic variability have been observed previously (Clark et al., 1999; Hare and Mantua, 2000; Hollowed et al., 2001; Lehodey et al., 2006; Yati et al., 2020). The analysis of Chhak and Di Lorenzo (2007) (as seen in Franks et al. (2013)) suggests that positive phases of the PDO (driven by a stronger and southward-displaced Aleutian low) are typically related to stronger downwelling conditions in the coastal Alaskan Gyre (e.g., in southeast Alaska, subarea 2C). In agreement with this result, we found a positive relationship between the PDO and model-based surface temperature: both are higher in the periods when the O32 abundance is elevated. Higher surface temperature leads to a reduction in O_2 solubility, which we observe as a negative surface O_2 and Φ anomaly in those periods of time where the PDO is positive (Figure

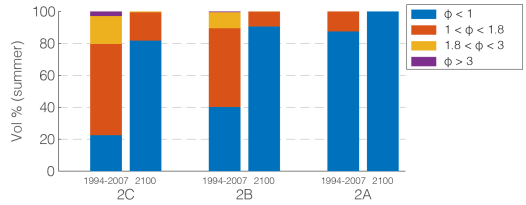

FIGURE 10 Volume fraction of several Φ classes in the deepest layer at each IPHC subarea (spatial distribution shown in Figure 9g,h), delimited by the 300 m isobath for the summer season. For each subarea, the summer climatology of years 1994-2007 is shown in the left column, and summer means of the future projection centered around year 2100 on the right.

S9).

Whereas the PDO is largely expressed in surface ocean waters, Pacific halibut will respond more directly to ocean conditions in their benthic habitat (Sadorus et al., 2014). However, we found that the relationship between PDO, temperature, O_2, and Φ observed at the surface is absent in the benthic habitat (Figure 8). Ocean bottom water properties seem particularly decoupled from the PDO index over the strong El Niño period from 1997-1998, with higher than usual temperature, O_2, and Φ, and a positive value of the PDO and the Ocenic Niño Index (ONI). El Niño is associated with stronger downwelling, indicating a potential interplay of subtropical and subarctic signals (Hollowed et al., 2001). This result suggests that the link between Pacific halibut abundance and the PDO index in subarea 2C reflects indirect mechanisms coupling surface and bottom waters, rather than changes in bottom water temperature, O_2 or Φ, per se.

Changes in mixed layer primary productivity could be a potential mechanism coupling surface water and benthic habitat, with higher productivity driving greater carbon export and higher benthic oxygen demand. To address this possibility, we used satellite-based time series of surface water chlorophyll concentrations as a proxy for phytoplankton biomass across our survey regions (not shown). This analysis did not reveal any clear relationship between surface chlorophyll and bottom water oxygen, Φ or Pacific halibut abundance. We are thus unable to provide a mechanistic explanation linking the PDO and halibut abundance. We note, however, that recent work has suggested that the coupling of the PDO with ecosystem processes has become weaker in recent years due to an overall weakening of the Aleutian low (Litzow et al., 2020).

4.2 | Future habitat availability

The spatial distribution of Pacific halibut is consistent with a spatial pattern of increasing ocean bottom oxygen and Φ from south to north in our study region. Based on the present day ecological Φ_{crit} distribution (Φ = 1), we were able to estimate future changes in suitable Pacific halibut habitat by the end of the century under a business-as-usual CO_2 emissions scenario. Under this scenario, it is projected that suitable Pacific halibut habitat will be restricted to the coastal region off Prince of Wales Island in subarea 2C by the end of the 21st century (Figure 9h). This habitat contraction is related to a projected decrease in bottom water oxygen and Φ.

In the California Current System, a combination of increased upwelling-favorable winds in spring, and increased stratification in summer are the main mechanisms for the strong oxygen decline, which drives much of the decrease in Φ (Howard et al., 2020a). Specifically, Howard et al. (2020b) attribute between 30 to 50% of the change to a decrease

in O_2 solubility in source waters, and the rest of the change to an increase in apparent oxygen utilization. A recent study by Dussin et al. (2019) found that combined changes in the nutrient and oxygen content of source waters might have a greater impact in the enhanced deoxygenation in the California Current than changes in upwelling winds alone.

Results from the future high CO_2 emissions simulation show that by the end of this century, the largest changes in temperature, oxygen and Φ are projected in subareas 2C and 2B at depths near 100 m (Figure S6), where Pacific halibut abundance is greatest (Figure S7). This change could have a disproportionate impact on the habitat environment of younger Pacific halibut (U32), which tend to live at shallower depths (Figure S7b), potentially pushing this size class towards more favorable regions either northward or nearer to the coast, following the general trend of other species around the globe (Sumaila et al. (2011), and references therein). It has been suggested, however, that Pacific halibut might exhibit a lateral, rather than vertical, redistribution in response to hypoxia events (Sadorus et al., 2014), supporting the idea of a northward migration. The waters of Hecate Strait (embedded in subarea 2B) are of particular interest, as a shallow region recognized as an important Pacific halibut spawning and nursery region (Loher and Wischniowski, 2008). Most of the Pacific halibut eggs spawned in this zone tend to settle there (Carpi et al., 2021), creating an important source of Pacific halibut for the local economy. This region will experience the most dramatic changes in the benthic habitat (Figure 9), with potential, but unknown repercussions for the regional Pacific halibut life cycle.

In the southernmost subarea (2A), low Φ values are already present near the coast due to summer upwelling. As a consequence, this region is projected to experience a less drastic change in Φ in comparison with subareas 2B and 2C. Instead, low values are projected to extend further offshore (Figure S6). Despite the small absolute change in Φ values by the end of the century in subarea 2A, future deoxygenation will potentially lead to the complete absence of suitable habitat for Pacific halibut in the US states of Washington and Oregon, limiting the US fishery to the state of Alaska. This potential habitat redistribution is in line with previous findings suggesting that climate change might lead to an increase in catch potential in the Arctic and subarctic regions (Cheung et al., 2010; Sumaila et al., 2011).

Given that a large percentage of the commercially-exploited marine species are shared between neighboring countries (Palacios-Abrantes et al., 2020), the potential shift in suitable Pacific halibut habitat to the north of the U.S.-Canada border might drive important economical (e.g., commercial and recreational fisheries) and societal (e.g., subsistence fishery) consequences for the Pacific halibut fisheries (Sumaila and VanderZwaag, 2020). Due to the projected northward displacement of suitable habitat, the potential positive impact on Pacific halibut fisheries off Alaska might be offset by other factors, e.g., reduced price due to the smaller size typically observed under higher temperatures, or a protein substitution (Sumaila et al., 2011). To precisely identify the economic impact, future studies could model the impact at a local level through integration of biophysical changes, fish population dynamics, and fisheries economics. Since Pacific halibut is a transboundary fish that migrates between the Exclusive Economic Zones of Canada (IPHC subarea 2B) and the U.S. (IPHC subareas 2A and 2C), the two countries co-manage the fish stock via the IPHC. The exact valuation of the shift in the fish distribution due to climate change can be a critical standard in addressing potential conflicts in co-management.

4.3 | Caveats

In interpreting our results, it is important to consider a number of complicating factors. Our simulations of habitat contraction are based solely on the present-day relationship between Pacific halibut abundance and oceanographic conditions, derived from a 17-year time series. However, other factors not considered in the future projections might play a role in defining the habitat of groundfish species. For example, Youcef et al. (2015) found that the potential negative impact of a reduction in oxygen concentration on Greenland halibut in the Gulf of St. Lawrence was compen-

sated by other factors such as food abundance, food availability, and/or predator density. It is possible, even likely, that similar mechanisms complicate the observed relationship between PDO and O32 in subarea 2C (and potentially explain why this relationship was not observed in other subareas). We also note that the domain of our future projection does not resolve temperature and oxygen changes in some coastal regions off British Columbia and other fjords in Southeast Alaska, where Pacific halibut abundance is low. Unknown future changes in habitat availability could exacerbate this trend, or open new habitat regions for Pacific halibut. Given the large degree of interconnectivity of Pacific halibut in the Northeast Pacific (Sadorus et al., 2021), future studies on climate change impacts would benefit from considering the full range of Pacific halibut distribution, for example by utilizing a high-resolution global earth system model. Continued sampling of oceanographic and fisheries-independent Pacific halibut abundance data will extend the observation-based time series of environmental variables, and contribute to a better understanding of the relationship between Pacific halibut interannual variability and oceanographic properties.

Finally, it is important to note that our future model projection is based on only one model and one potential future scenario (RCP8.5). Alternative scenarios have been shown to generate significant differences in the projected future distributions of several groundfish in the Eastern Bering Sea (Rooper et al., 2020). The actual impacts of future ocean warming and deoxygenation on Pacific halibut and other fisheries abundance will thus depend directly on the approaches used to curb global greenhouse gas emissions, harvest regulations, as well as climate change adaptation policies (Sumaila et al., 2019).

5 | CONCLUSIONS

Using a combination of observations and model simulations, we derive an index of Pacific halibut habitat suitability for active metabolism (Φ) based on the relationship between environmental oxygen supply and biogeographically-derived ecophysiological traits. By including information from a decadal time series of Pacific halibut CPUE, we show that interannual variability in Pacific halibut CPUE in the northernmost region (off Prince of Wales Island) may be coherent with the Pacific Decadal Oscillation. In contrast, the PDO shows no significant association with the near ocean bottom Φ, suggesting that the PDO relationship with Pacific halibut CPUE might reflect an indirect coupling. Future projections of ocean deoxygenation and warming are expected to lead to a reduction in suitable habitat for Pacific halibut, particularly in the southernmost region analyzed here (subarea 2A). A shift of approximately five degrees northward of suitable habitat will likely lead to a northward displacement of Pacific halibut populations. Further work with bioeconomic models might unveil potentially strong implications for ecosystems and fisheries.

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